ON THE OSSIFICATION OF THE VERTEBRÆ IN THE WOMBAT AND OTHER MARSUPIALS.

By R. Broom, M.D., B.Sc.

(Plate xlix.)

During the course of development there may be recognised many ancestral characters which are either quite lost or greatly obscured in the adult forms. In the adult of the human species only the dorsal vertebræ have distinct ribs, yet during the early stages of development there are clear indications of elements homologous with ribs in the first three sacral vertebræ and in at least the seventh cervical. As in the ancestral reptilian condition well developed pleurapophysial elements were attached to practically all the vertebræ, it is but natural that further indications should be met with in the development of the vertebræ of the lower mammals.

On looking into the mode of ossification of the vertebræ in the marsupials, I have come across one or two interesting points in which the condition differs from that ordinarily found in the higher mammals.

Cervical Vertebræ.—The atlas vertebra in the marsupials, as is well known, differs from that in the higher mammals in the lower piece being in some forms very small and in many others quite absent. In the monotremes the inferior element is well developed as in the higher forms, and in the more primitive marsupials such as the Dasyures, a well developed osseous element unites the two arches below. Though this is the condition in the majority of the Polyprotodonts, the intermediate piece is very small in certain species of *Perameles*, and even in *Thylacinus* is quite narrow. In the smaller Diprotodonts (*e.g. Petaurus breviceps*) a small intermediate piece is present which almost exactly resembles that in certain species of *Perameles*. In

Trichosurus the two arches meet inferiorly without a third element, but occasionally a rudimentary inferior element is present. In the smaller wallabies the arches meet as in *Trichosurus*. In the larger wallabies and kangaroos, in the wombat, in *Phascolarctus*, and in the large extinct Diprotodonts, there is a more or less wide gap between the lower ends of the arches bridged by fibrous tissue. It would seem as if in the smaller and ancestral Diprotodonts the intermediate piece had become gradually reduced in size until it became lost, and that as the Diprotodonts increased in size the arches became again separated, the place of the lost intermediate piece being taken by fibrous tissue.

The axis vertebra is very similar in structure to that in the higher forms. There is, however, one interesting point of difference in the development, in that whereas in man, and probably most of the higher mammals, the odontoid process is ossified from a pair of centres, in the marsupials there is but a single median centre as in the centra of the more normal vertebræ.

The cervical vertebræ from the 3rd to the 7th are ossified from three centres—one for the body and one for each arch. I have been unable to find any ossification which could be regarded as a costal element.

Dorso-lumbar Vertebræ.—The dorsal vertebræ are developed similarly to those in the higher mammals; and in the majority of marsupials the same may be said of the lumbar vertebræ. In the wombat (*Phascolomys mitchelli*), however, a remarkably interesting exceptional condition is met with. The first three lumbar vertebræ are developed from three centres as in man, but the fourth lumbar vertebra differs in having well marked autogenous transverse processes. In figs. 2-3 of Plate xlix., are shown anterior and upper views of the fourth lumbar vertebra of a half grown wombat. When compared with the third lumbar vertebra (fig. 1), the only difference of any importance is that seen in the condition of the transverse processes. In the third vertebra there is a fairly large transverse process developed exogenously from the arch, while in the fourth vertebra there is a small transverse

process developed from the arch to which is articulated an independent additional element—an autogenous transverse process. According to Flower* the transverse processes of the anterior lumbar vertebræ of the pig are originally autogenous elements though coalescing very early with the rest of the vertebræ, and in certain cetaceans the transverse processes of the lumbar vertebræ are autogenous elements. In many reptiles, and especially in those reptiles from which the mammals appear to have sprung—the Theriodonts—all the trunk vertebræ have costal elements, and in the lower trunk or lumbar region these elements are articulated to the vertebræ exactly as are the autogenous processes in the wombat. Fig. 4 represents the upper side of a lower trunk vertebra of *Cynognathus*, and if this be compared with the fourth lumbar of the wombat (fig. 3) it will be seen that the two agree closely except in the different degree of development of the parts, and that there is no reasonable doubt but that the rib-like appendages of the vertebra of *Cynognathus* are homologous with the autogenous transverse processes of the vertebra of the wombat.

Sacro-caudal Vertebræ.—In the human subject the term "sacrum" is applied to the anchylosed five vertebræ which support the pelvic bones. Here there is no difficulty in defining the limits of the sacral series of vertebræ, and in many other mammals the difficulty is no greater. There are many forms, however, in which not only are a different number of vertebræ anchylosed in different individuals, but where even in the one individual the number increases as age advances. According to Flower, "a more certain criterion is derived from the fact that some of the anterior vertebræ of the sacral region have distinct additional (pleurapophysial) centres of ossification, between the body and the ilium. To these, perhaps, the term *sacral* ought properly to be restricted, the remaining anchylosed vertebræ being called *pseudo-sacral*, as suggested by Gegenbaur." If this criterion, however, be applied to the sacrum of the marsupials it

* W. H. Flower, "Osteology of the Mammalia."

will be found at once to break down, since in most marsupials the upper caudal vertebræ have well developed autogenous transverse processes which are undoubtedly serially homologous with the pleurapophysial centres of those vertebræ which support the pelvic bones.

If the fifth vertebra of the sacro-caudal series of a half-grown wombat be examined (fig. 9) it will be seen to be made up of a well developed flattened centrum and a feebly developed arch, with on each side a rather large, flattened autogenous transverse process. The transverse processes articulate mainly with the centrum, but also with the arches. A similar description would apply to the 6th, 7th, and 8th vertebræ, but on reaching the 9th the transverse process is found to articulate only with the centrum. On passing forwards the 4th vertebra is found to be very similar to the 5th, while the 3rd differs only in the slightly increased development of the arch and of the transverse processes. The second vertebra, which is usually regarded as a true sacral vertebra, has the transverse processes strongly developed for articulation with the ilia. In the first vertebra of the sacro-caudal series the elements are exactly the same as in the fifth vertebra and only differ in being larger, and in having the arch proportionately more largely developed, and in having the lateral elements specialised for the support of the pelvic bones. In fig. 5 is shown a front view of the first sacro-caudal vertebra, and well displaying the distinctness of the lateral elements. In fig. 6 is seen a similar view of the first sacro-caudal vertebra of *Deuterosaurus*, where the lateral element remains distinct apparently throughout life.

In *Didelphys* the condition is very similar to that in *Phascolomys*, as may be seen in fig. 10 ; the transverse processes, however, of the caudal vertebræ are scarcely so well developed.

In *Macropus* the first two vertebræ have well-developed lateral elements ; the third has the lateral element small but distinct ; the fourth has a large autogenous process ; while the fifth has a small autogenous process. The other vertebræ of the series do not appear to have autogenous processes.

In *Trichosurus* the first two vertebræ have large autogenous lateral elements, and a considerable number of the succeeding vertebræ have small autogenous transverse processes.

As the lateral pleurapophysial elements of the first sacral vertebra are thus seen to be homologous with the autogenous lateral elements of the succeeding vertebræ, it becomes quite impossible to draw a distinction between sacral and caudal vertebræ by the criterion above referred to.

In the manati and the beaver among Eutherians the transverse processes of the caudal vertebræ are developed autogenously; but Flower doubts if "this circumstance alone is sufficient to entitle them to be considered as costal elements." From the marsupial condition it is manifest that the caudal transverse elements are homologous with the lateral elements of the first sacral vertebra, and as it is pretty well established by comparative anatomy that the lateral elements of the sacrum are modified ribs, we are forced to the conclusion that the autogenous transverse processes of the upper caudal vertebræ in the marsupials are really costal elements.

EXPLANATION OF PLATE XLIX.

Fig. 1.—Front view of 3rd lumbar vertebra of half-grown wombat.
Fig. 2.—Front view of 4th lumbar vertebra of half-grown wombat.
Fig. 3.—Upper view of 4th lumbar vertebra of half-grown wombat.
Fig. 4.—Upper view of a lower trunk or lumbar vertebra of *Cynognathus* (reduced; modified from Seeley).
Fig. 5.—Front view of 1st sacro-caudal vertebra of half-grown wombat.
Fig. 6.—Front view of 1st sacro-caudal vertebra of *Deuterosaurus* (reduced; modified from Seeley).
Fig. 7.—Under view of 1st sacro-caudal vertebra of half-grown wombat.
Fig. 8.—Under view of 5th and 6th sacro-caudal vertebræ of half-grown wombat.
Fig. 9.—Under view of 2nd, 3rd, and 4th sacro-caudal vertebræ of half-grown wombat.
Fig. 10.—Under view of first four sacro-caudal vertebræ of young *Didelphys* (× 4).